

A SECOND SPECIMEN OF WYULDA SQUAMICAUDATA ALEXANDER

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PLATES X AND XI

To the courtesy of the Rev. J. R. B. Love, formerly of Kunmunya Mission in the Kimberley Division of Western Australia, I owe a field skin and skull of this interesting marsupial, which apparently has not been taken since the description of the single type specimen by Alexander in 1918.

The locality is about 150 miles north-west of that of the type and upon the opposite coast of the peninsula. Mr. Love reports that the Worora blacks call it Ilangurra, and state that it lives amongst rocks and occurs throughout all their country as far as Obagooma, near Derby, 250 miles south-west of the Mission.

Mr. Alexander (1) justly remarks at the close of his careful description and summary that the generic or subgeneric arrangement of *Wyulda* and its allies, *Phalanger* and *Trichosurus* stands in need of review with more adequate material. This desideratum may be long delayed but the time seems opportune to re-examine the former animal as far as may be, with the aid of this new example.

In general a close agreement with the types has been found, but there are some discrepancies, and needful additions and amplifications have been made, with a review of its phylogenetic position. In the following description, from motives of convenience and brevity, direct comparisons are usually made with *Trichosurus*, but without prejudice of affinity.

External Characters

These cannot, of course, be checked with accuracy from the filled skin. The approximate dimensions are: head and body, 427 mm.; tail, 330; pes, 49; ear, 28. The ear measurement would probably be at least 25% greater in the flesh—approximately 35 mm. The ratio of head and body length to tail length is about as in *T. vulpecula*, and in many species of *Phalanger* as well.

In life the superficial aspect of the animal would probably justify the use of the vernacular *Cus Cus* already applied to it by Longman (3). Head short and wide, with the muzzle region rather weaker than in *Trichosurus* but less conical and pointed than in *Phalanger*. All facial vibrissae are strongly developed and entirely black; the mystacial reach 73 mm., the genals 62 and the supraorbitals 57 mm. Rhinarium large, naked and its surface finely granular; it has a well marked median groove with a small projecting process at its base as in *Trichosurus*.

Limbs noticeably shorter than in *Trichosurus*; vibrissae well developed on forelimb; ulna carpal and anconeal white; medial antebrachial black; they are more conspicuous than in *Trichosurus* owing to the shorter coat. The calcaneal set also present and white.

The manus is shrunk but seems small for the size of the animal. Digital formula $4 > 3 > 5 \geq 2 > 1$, as given for the type. This, while agreeing with the condition quoted for *Phalanger*, is not unknown in *Trichosurus*, where, however, $4 > 3 > 2 > 5 > 1$ is more usual. The claws are short, not strongly curved, nearly obscured by the fringing hairs of the digits, and (in the dried state) scarcely projecting beyond the apical pads. In the flesh their saliency would be still further reduced and their piercing and prehensile effectiveness much inferior to that of either *Trichosurus* or *Phalanger*. The apical and palmar pads are in relative development and shape quite similar to *Trichosurus*, but the surface, particularly of the latter elements, is marked by transverse parallel or concentric striae, more continuous and less granular than in that genus, but quite similar to the condition to be seen in dried skins of *Phalanger maculatus* and *P. breviceps*.

In the *pes* the general condition seems very close to *Trichosurus*; the pads about as well developed and with similar shapes, though evidence of special affinity to either *Phalanger* or *Trichosurus* can scarcely be looked for here, since Bensley (2) has shown that the condition overlaps in the two genera. In the dried condition, however, the pads in *Wyulda* are more conspicuous than in the latter owing to their finer striation. The claws are relatively longer and sharper than on the manus.

Tail as in the original description, but the basal portion is densely furred like the back (not scantily, as stated), and the transition to the tubercular portion is abrupt and linear. The tubercles increase in size and prominence towards the middle reaches of its length and then fall away distally again, though they are everywhere very distinct. Their arrangement is such that they fall into well-marked linear series, crossing the tail surface obliquely at an angle of 40° to its midline. Measured along the dorsal midline their frequency increases from four to six per cm. The interscalar spaces are beset with black bristle hairs, averaging three per scale and about one-half of a scale in length, and visible only on close inspection. On the distal half of the ventral surface of the tail, the chief site of the prehensile function is free from tubercles and transversely creased, a condition present in both *Trichosurus* and at least some *Phalanger* species also.

In the material of *Phalanger* available to me there is little in the caudal scalation of the dorsal surface to recall that of *Wyulda*, but on the ventral surface of some examples of *P. maculatus* just proximad of the prehensile area, low but distinct and very separate tubercles are developed in transverse rows of five, separated by the width of two—a condition which might be regarded as an incipient phase of that of *Wyulda*. Alexander suggests that the nudity of the tail is a primitive character, and quotes in support the individual variation in the scale development in some species of *Phalanger*. This is difficult to disprove, but it seems more probable that the loss of hair is a recent change made in response to a newly acquired habit of rock climbing. There is some slight support for this in the analogous case of *Pseudochirus dahli*, and still more in the specialised condition of the scales which differ widely in their roughened, tubercular and protuberant character, from those of *Hypsiprymnodon* the only primitive marsupial with which direct comparison is possible.

Pelage

Very short, fine, soft and copious. Constitution of pelage, vertical distribution of colour and general appearance of coat quite like some of the northern and central forms of *T. vulpecula*; the fur duller and without the sparkle and gloss of the southern animal, or of most species of *Phalanger*. Mid-dorsally the main pile reaches 12 mm. with a sparse overlay reaching 16 mm. Here the basal half of the fur is Pale Neutral Grey, the succeeding quarter a pale slightly vinaceous brown near Wood Brown, the subterminal band ashy—near Tilleul Buff—and the extreme tips and guard hairs black. Towards the rump the basal colour becomes warmer and more ochraceous and the brown zone tends to merge with the base.

The general dorsal colour is a pale ashy grey finely grizzled and obscurely mottled on the nape, shoulders and rump with washes of buff. The head and mid-back are coldest in tone and are near Neutral Grey. The buffy areas are inconspicuous and bear no relation to the strong rufosity of fore-quarters common in similarly aged males of *T. vulpecula*. The overlay of black is slight except mid-dorsally where an obscure stripe is developed. Sides like the back, but somewhat paler and less grizzled, though still mottled irregularly with buff. Ventral fur creamy white to base except on throat and chest, where it is Pallid Neutral Grey; external colour creamy white mottled with pale buff. Scrotum nearly nude. Head pure cold grey like the midback, muzzle upper lip and orbital ring weakly washed with brown, but not strongly contrasted as in *Trichosurus* and without the dark chin patch. Ears nearly nude internally, externally rich brown (Bistre) at base,

elsewhere very sparsely clad with greyish-white; the bases strongly contrasted with the head. Limbs externally like sides, internally like belly, but with a slightly warmer tone, especially on the hind limbs where the basal colour is pale ochraceous buff. Manus and pes uniform greyish-brown, near Pale Drab, and not strongly contrasted with the limb.

From the original illustration (*loc. cit.*) the present specimen differs in the much paler and colder dorsal colour, whiter ventral colour and inferior lateral demarcation except posteriorly towards the hind limb, where it is abrupt; from Cayley's, fig. 1, pl. x, in Troughton's "Furred Animals of Australia" (1941) it differs in lacking the strong reddening of head and limbs.

Skull

This gives the following dimensions in mm. (those of the type follow them in brackets): basal length 74.1, (73); greatest breadth 51.4, (54); nasals length 31.2 (29); nasals greatest breadth 14.4, (14.5); nasals least breadth 7.3 (10.3); constriction breadth 9.6,⁽¹⁾ (8.7); palate length 43 ca., (33); palate breadth outside M² 23.5, (23); palate breadth inside M² 14.2, (15.2); anterior palatine foramina 5.5, (5.5); basicranial axis 25.3, (24.5); basifacial axis 48.4, (48.5); facial index 191, (198); horizontal length of P⁴ 5.0,⁽²⁾ (4.7); length M^{s1-3} 12.1, (12.5); length of lower I, 13.9, (12.0).

Important discrepancies are shown only in the least breadth of nasals, and palate length; and in both cases the type description seems erroneous as the illustrations do not support them, but give measurements agreeing closely with my own.

In general dorsal outline and many structural features the skull is close to *Trichosurus*; under the first head the chief differences lie in the relatively greater posterior width, and the attendant change in shape of the zygomatic arch, the posterior width of which is markedly superior to the anterior or middle width. This is an accentuation of a condition already present in *Trichosurus*, whereas in *Phalanger* anterior and posterior width are usually equal or the anterior even greater.

Other respects in which resemblance is shown to the former rather than the latter genus are as follows:

- (1) The muzzle region generally is even narrower and more slender than in *Trichosurus*; the nasals project beyond the naso-maxillary suture and overlap the gnathion; the premaxillae make a larger contribution to the wall of the nares than the maxillae.
- (2) Greater development of the post-orbital process of the jugal.
- (3) Detailed condition of the braincase and its rugosities and the lambdoid and sagittal crests.
- (4) The upper profile, which ascends steadily and evenly from the nasion to a vertex in the sagittal crest just anterior to the auditory meatus and without bulging in the frontal region.
- (5) The condition of the squamous temporal which is inflated both in its dorsal and occipital aspects, to a degree unequalled in the recent Phalangeridae. In relation to *Trichosurus* it presents no novel features, however, except that of degree—the three species *T. caninus*, *T. vulpecula* and *Wyulda* forming a progression in this, while in *Phalanger* it is markedly less.
- (6) At the base of the skull the auditory bulla presents features of interest. Its degree of expansion is intermediate between that of *T. vulpecula* and *T. caninus*, and therefore much greater than in *Phalanger* where the parts are scarcely raised. The bulla shows a tendency towards the more primitive bilobed condition found in *Petaurus* and *Dromicia*, being

⁽¹⁾ On supraorbital edges; below them, 7.5.

⁽²⁾ Maximum diameter along oblique axis, 5.6.

divided by a shallow oblique sulcus into two moieties. But whereas in these genera both moieties are contributed by the alisphenoid, in *Wyulda* only the postero-internal element is so derived while the antero-external portion, which is the more prominent of the two, is formed from a ventral process of the squamosal descending from the floor of the glenoid fossa. This arrangement seems to be unique in the Phalangeridae, though it is fore-shadowed in a small percentage of skulls of *T. vulpecula*.

In the original description of the type, the bullae were stated to be very large and responsible for the great posterior width of the skull; this, however, is only true if the mastoid process of the periotic is regarded as part of the bulla, and for this there seems no justification at all. Anteriorly the mastoid is well separated from the alisphenoid-squamosal bulla as defined above, and posteriorly its contours blend completely and without demarcation with the general occipital cellular inflation.

Some other points in which it shows differences of a minor kind from either *Trichosurus* or both genera, concern the hard palate which anteriorly is less rugose than in either and the interorbital concavity which favours *P. orientalis* in shape.

Finally, the expansion of the mastoid process of the periotic is responsible for another peculiarity of the skull—namely, the great reduction in the paraoccipital process of the exoccipitals. In the caudad view these prongs are pressed against the mastoids and squamosals almost throughout their entire length, and scarcely project as free elements at all; in the two allied genera they project prominently.

Mandible

Likeness to *Phalanger*, especially to the smaller species, is more readily traceable here than in the skull. The area of the ascending portion of the ramus with respect to the body is less than in *Trichosurus*, the condyle is set lower, the coronoid process rises higher and its anterior margin slopes back at a greater angle, and the symphysis is slightly shorter. The general condition of the masseteric fossa and of the condyle itself is much as in *Trichosurus*, but the inflected angle differs from both the related genera, in being less acute at the extremity and its medial margin is not recurved ventrally to form a flange; the floor of the pterygoid fossa differs correspondingly.

Dentition

Incisors—The upper incisors in the present example differ considerably from those of the type, the differences being partly due perhaps to the greater wear of the former. I^1 which was stated by Alexander to be nearly cylindrical has here an antero-posterior width at the alveolar margin nearly twice its transverse width, and much of its disproportion as compared with I^2 would seem to be due to the relatively much greater wear on the latter. I^3 in this example could never have reached two-thirds the size of I^1 at any stage of wear, though it is to be noted that in the tabular summary of characters of the type it is said to be "moderate," as in *Trichosurus*; in the latter it averages nearer one-third of I^1 .

In general, when compared with similarly worn examples of *T. vulpecula*, the agreements are much more notable than the differences. This is particularly so in the upright setting of the incisors in the premaxillae and the loss of all tendency to procumbency, and in the close proximation of the first incisors to one another in the midline. The first lower incisors are relatively slightly longer than in *Trichosurus*, narrower and less spatulate and they ascend towards their occlusion with their upper opponents, at a slightly steeper angle; sympathetically the incisor-premolar diastema is shortened. Two lower vestigial incisors are present as in the type; the anterior procumbent, the other upright.

The incisors as a whole therefore, especially in the lower jaw, are slightly more primitive than in *Trichosurus*, but show very little special resemblance to *Phalanger*.

The canine, in size and situation, is exactly as in *Trichosurus*, but is slightly sharper and more strongly curved.

Premolars—Upper P^1 about one-half of the size of the canine and similar in size, shape and position to *T. vulpecula*, in its usual condition, though there is some variation in the latter. Median upper premolar quite absent. The upper P^4 is a remarkably large tooth, exceeding any of the molars in sectional area and greatly exceeding them in bulk. It exhibits strong sectorial specializations, actually exceeding in some respects those of *Trichosurus*, but in detailed morphology is intermediate between that genus and the more advanced forms of *Phalanger*, cf. *lululae* and *rothschildi*, as described. The crown of the tooth, both cone and blade, projects far below the crown surface of the molars. The outer surface of the blade is concave, a shallow but well-defined sub-triangular fossette occupying the greater part of its area, while the upper portion is marked by three prominent narrow vertical grooves, extending to the cutting edge which is correspondingly serrate; and vestiges of a parallel series are to be seen upon the antero-internal face. Almost the whole area of the latter is occupied by an occlusal facet of greater extent and more even development than in *Trichosurus*. The tooth is rotated outward to a marked degree, probably more strongly than in any other recent marsupial, and its cutting edge makes an angle of about 45° with the long axis of the molar series; a line drawn along its cutting edge, if produced, bisects the crown of M^4 . The lower P_4 also larger than any of the lower molars, and similarly rotated, grooved and worn. As in the type a vestigial premolar is pressed against the base of P^4 .

Molars generally very close to those of *Trichosurus*. In sectional area the sequence in the upper series is $M^1 = M^2 > M^3 > M^4$, and in the lower $M_2 = M_3 > M_1 > M_4$; both formulae agreeing with *Trichosurus* except that in *T. caninus* M^4 may be equal to M^1 . The declension in size of the posterior molars, both above and below, is steeper in *Wyulda* than in *Trichosurus*, and much steeper than in the species of *Phalanger* to which I have access, in which there is a marked tendency towards the enlargement of the third and fourth molars both above and below, leading to subequality of the upper molars, and in the lower jaw even to such formulae as $M_4 > M_3 > M_2 > M_1$.

The molars are slightly broader in relation to their antero-posterior length than in *T. vulpecula* and their over-all shape is rather less quadrate, the width of the posterior of M^2 and M^3 being about one-third less than that of the anterior; in both respects they approach *T. caninus* more closely than *T. vulpecula*. The molar enamel is smooth and free from the pitting and marginal crenulation frequent in *Phalanger*. The lingual cusps are slightly less elaborated than in *Trichosurus* but in all structural detail of significance, such as the longitudinal linking of the lingual cusps, development of anterior and posterior terminal ledges, transverse ridging of the buccal cusps, exaggeration of the paracone on M^1 and the wearing pattern, there is a very close agreement with that genus.

The dentition as a whole, therefore, resembles *Trichosurus* more closely than *Phalanger*. Traces of more primitive conditions linger in the lower incisors and canine, but the complex of characters which marks the progressive herbivorous evolution of the subfamily, and in which the former is held to be more advanced are either equally developed in *Wyulda*, or in some respects carried still further.

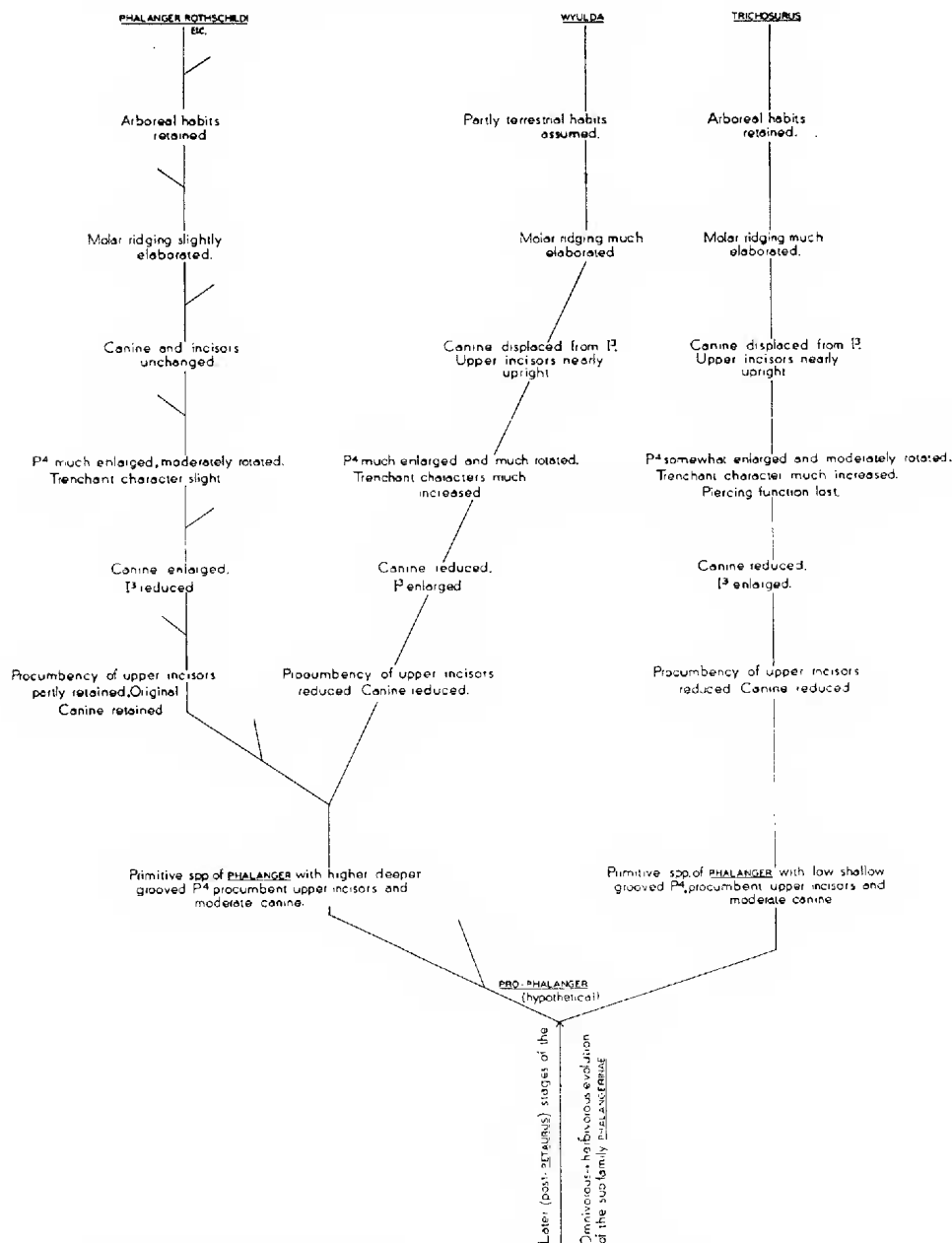
Relationships

Setting aside a considerable substratum of characters in which an intermediate conditions is shown, the status of *Wyulda* in the matters here reviewed may be roughly summarised in the following categories:

- 1 Resemblances to *Trichosurus*:
 - (a) general structure of skull; (b) general level of dentition; (c) pelage.
- 2 Resemblances to *Phalanger*:
 - (a) digital formula; (b) striation of pads; (c) tail (in origin); (d) mandible (in part); (e) lower incisors, canine and P^4 (in part).

3 Characters in which *Wyulda* is peculiar or shows an extreme development of a condition already present in either *Phalanger* or *Trichosurus*:

- (a) reduction of forelimb and manus; (b) loss of piercing specialisations in the claws of manus; (c) tail (in detail); (d) bulla (in detail); (e) inflation of temporals; (f) paraoccipital processes; (g) axial rotation and wear of P^4 ; (h) molar gradation; (i) condition of mandibular angle; (j) petrophile habit.



The somewhat heterogeneous character of *Phalanger*, containing as it does several incipient specialisations more or less divergent, creates a taxonomic problem which Alexander in his discussion (*op. cit.*) opines may best be solved by the recognition of subgenera therein. In suggesting the inclusion of *Trichosurus*

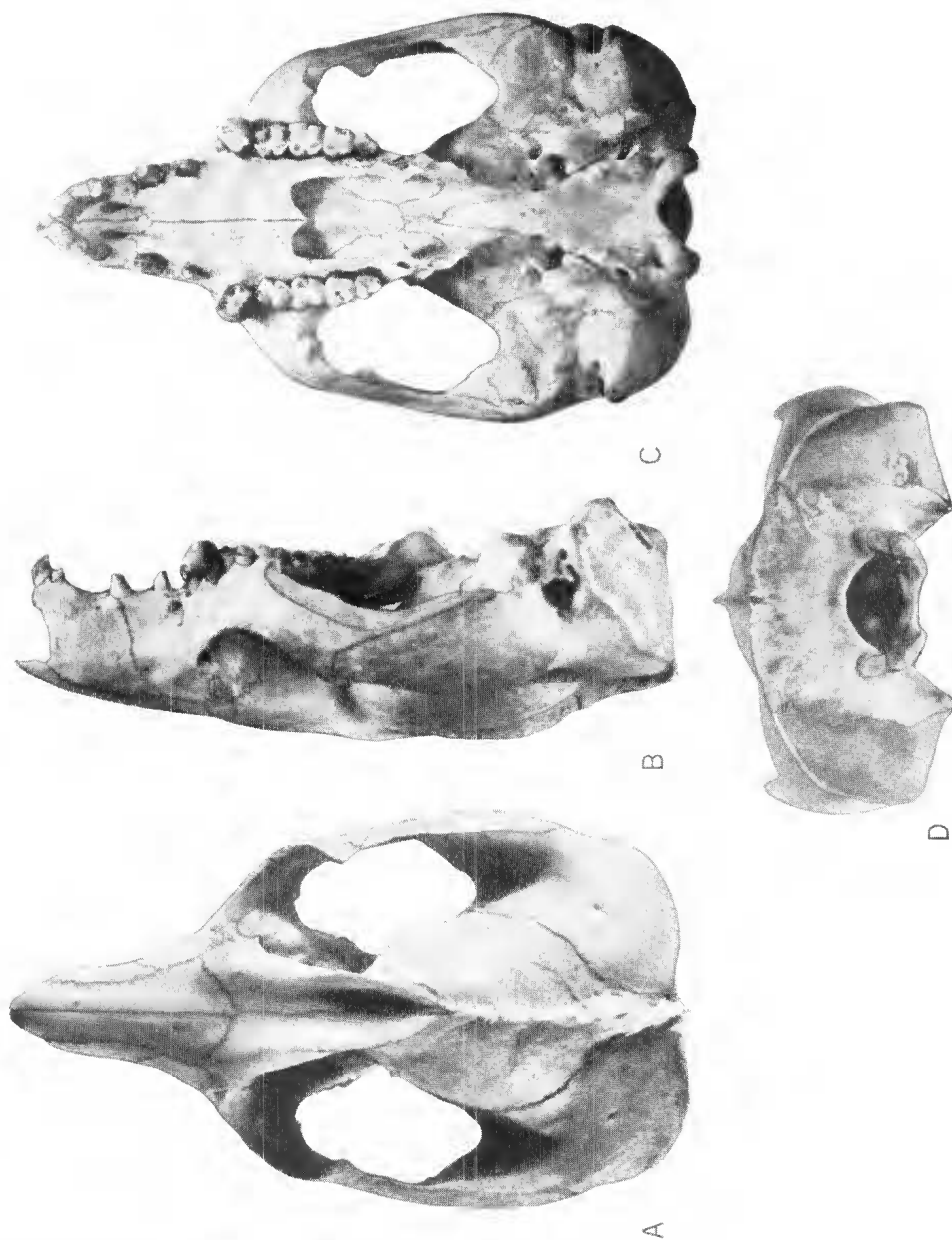


Photo by H. H. Finlayson

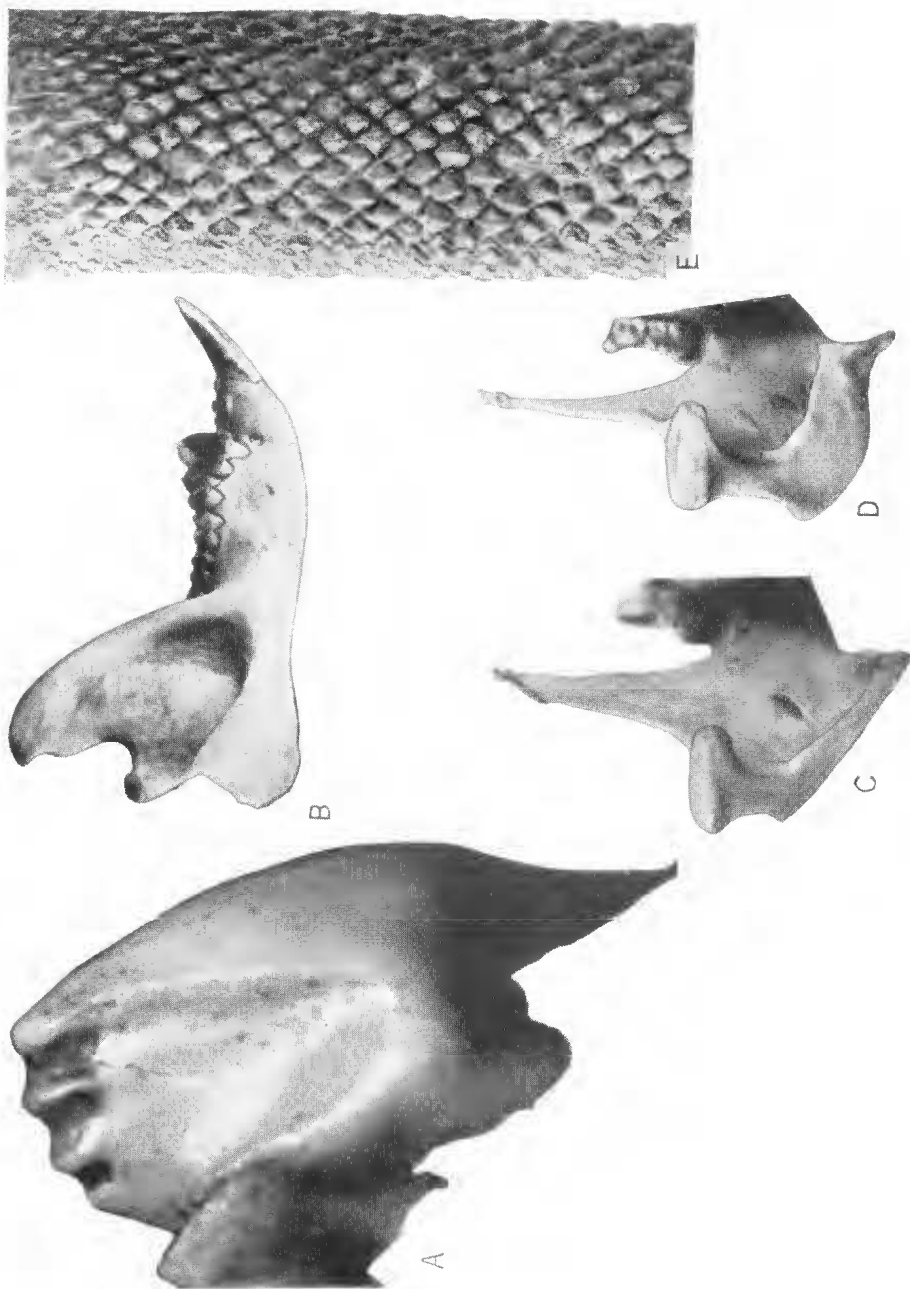


Photo by H. H. Finlayson

in this scheme of subgenera, however, he has evidently overlooked the fact established by Bensley with ample material for comparison that the *Trichosurus* dentition as compared with that of any of the numerous forms of *Phalanger* represents a distinct advance in the herbivorous specialisation which is the major theme in the evolution of the subfamily.

In the same way, it would not appear from the results of the present detailed examination, that *Wyulda* (despite some basic resemblances especially in plastic characters) differs very widely from any of the species of *Phalanger*, and that even the most conservative view could scarcely withhold generic rank from a species presenting such a complex of differential characters as is listed at (3) above.

The resemblances to *Trichosurus* are striking, but any derivation of *Wyulda* from that genus, either by retrogression or further evolution, is clearly ruled out by the evidence of the posterior premolars. This leaves as the obvious alternative an independent collateral development of both from ancestral forms of *Phalanger* which differed in premolar character in somewhat the same way as the Bettongiinae do from the Macropodinae.

On this view the evolution of the three genera, as interpreted by dentition alone, might be represented somewhat as in the scheme on page 260.

The dental evolution of *Phalanger* and *Trichosurus* is closely associated with an arboreal habit in all the species of both, and is phytophagous rather than herbivorous in the wider terrestrial sense. Since the dentition of *Wyulda* is on much the same phytophagous level as *Trichosurus*, it would appear that the present partly terrestrial rock haunting habits of the former represent a recent development, initiated possibly by the desiccation of the habitat, and that the response to this has so far only affected the plastic anatomy of the forelimb and manus and possibly the tail.

Regarding the caudal depilation, Mr. Love informs me (*in litt.*) that the Worora have views of their own. It came to pass in this way. Long ago, in the early time, Ilangurra had a bushy tail like Burkumba the ordinary opossum. One day when Ilangurra was beginning to climb into a tree, a passing echidna, Koonunginya, in mischievous mood, siezed him by the tail and tried to pull him down. He did not succeed but instead pulled all the hair out of the tail. Thereupon Ilangurra jumped down and in a rage seized Koonunginya and threw him into a prickly bush. Since that day of discord Ilangurra has had a bare and scaly tail and Koonunginya has been covered with spines.

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EXPLANATION OF PLATES X AND XI

PLATE X

Fig. A, B, C, D—Dorsal, lateral, palatal and occipital aspects of the skull of *Wyulda squamicaudata* Alexander, adult ♂ from Kunmunya. (x1 ca.)

PLATE XI

Fig. A—Upper posterior premolar of the left side of *Wyulda squamicaudata* Alexander. Adult ♂ from Kunmunya; a postero-external view of the blade at about 90° to the cutting edge, with the paracone of M¹ in situ. (x11 ca.) Fig. B—Lateral view of mandible. (x1.1 ca.) Fig. C—Posterior view of same to show condition of the inflected angle and pterygoid fossa. (x1.8 ca.) Fig. D—Ditto in *Trichosurus vulpecula*. (x1.4 ca.) Fig. E—Proximal portion of dorsal surface of the tail of *Wyulda squamicaudata* Alexander. (x2 ca.)